

A PUZZLING NEW SNAKE (REPTILIA: SERPENTES)  
FROM THE LATE PALEOCENE OF MISSISSIPPIJ. ALAN HOLMAN<sup>1</sup>GERARD R. CASE<sup>2</sup>

## ABSTRACT

A puzzling new genus and species of primitive alethinophidian snake, *Tuscahomaophis leggetti*, is described on the basis of vertebrae from the late Paleocene Tuscahoma Formation of Meridian, Mississippi. *Tuscahomaophis* has characters on the centrum, condyle, hypapophysis, neural arch, and prezygapophyses that indicate relationships to the Palaeophiidae and, to a lesser extent, the Nigerophiidae and distinguish it from other primitive alethinophidians. But *Tuscahomaophis* differs from the above two families in the location of the paradiapophyses, characters on the ventral centrum and neural arch, and in having parazygantral foramina that occur in small fossae. Curiously, the parazygantral character is unique to the Madtsoiidae (and one other undescribed snake) and is considered to be apomorphic in each of these taxa.

At present it seems best to suggest that *Tuscahomaophis* is a sister group of the Palaeophiidae, that the Nigerophiidae is a sister group to both of the former; and that *Tuscahomaophis* has independently developed the parazygantral character of the Madtsoiidae. The new snake is assigned to the suborder Alethinophidia, family *incertae sedis*. *Tuscahomaophis* may have been an aquatic snake that occupied a riverine or an estuarine habitat.

## INTRODUCTION

In April 1990 a field party from the Carnegie Museum of Natural History led by K. C. Beard collected the vertebral remains of a new genus and species of primitive alethinophidian snake from the upper part of the Tuscahoma Formation in Meridian, Mississippi. The new form is puzzling, as it has a suite of characters that indicate it is most similar to the Palaeophiidae and somewhat less similar to the Nigerophiidae; one character that is unique to the Madtsoiidae (and one other undescribed snake); and other characters that distinguish it from all three families. Here we describe this new taxon and discuss its relationships.

*The Tuscahoma Formation.*—The upper part of the Tuscahoma Formation at Meridian, Mississippi, has previously been referred to the early Eocene (Case, 1986; Dockery et al., 1991; Parmley and Case, 1988:334), but new evidence (Ingram, 1991) suggests that the sediments that yielded the new snake described below are of latest Paleocene age.

The Tuscahoma Formation at the Meridian, Mississippi, site (CM loc. 517; see Beard and Tabrum, 1991) is overlain by the fossiliferous Bashi Formation. CM loc. 517 is the first known vertebrate site in the Tuscahoma Formation, and likely represents an estuarine or riverine deposit, as it contains the teeth, scales, vertebrae, spines, etc., of a large variety of fishes including numerous species of selachians (Case, 1986). The fauna also includes a variety of tetrapods including mammals, birds, lizards, crocodylians, turtles, the presently described new primitive alethinophidian snake, and three species of palaeophiid snakes: *Palaeophis*

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*casei* Holman, *P. virginianus* Lynn, and *P. littoralis* Cope (Holman, 1982; Parmley and Case, 1988; Holman et al., 1991).

Abbreviations are: CM, Carnegie Museum of Natural History; MSUVP, Michigan State University.

#### SYSTEMATIC PALEONTOLOGY

Order Serpentes Linnaeus, 1758

Suborder Alethinophidia Nopsca, 1923

Family incertae sedis

*Tuscahomaophis*, new genus

*Diagnosis.*—Similar to primitive alethinophidian snakes in having: a short, robust vertebral form; a massive zygosphenes and zygantrum; a thick, short neural spine; a large cotyle and condyle; and lacking prezygapophyseal accessory processes.

Most similar to Palaeophiidae and, to a lesser extent, the Nigerophiidae. Similar to both in having: condylar axis horizontal or only slightly oblique; roof of zygantrum structurally simple; lateral walls of posterior neural arch almost vertical; prezygapophyseal articular facets small and obliquely oriented; and prezygapophyseal buttresses with a sharp, anterolateral border running from the anterodorsal border of the paradiapophyses to the anterolateral tip of the prezygapophyses, and projecting anterolaterally beyond the prezygapophyseal articular facets.

Similar to Palaeophiidae and differs from Nigerophiidae in having: a shorter vertebral form; a relatively smooth, unexcavated ventral centrum; a small hypapophysis confined to the posterior extent of the ventral centrum; and a depressed neural arch. Resembles the Nigerophiidae and differs from the Palaeophiidae in lacking pterapophyses.

Differs from both families in having: the paradiapophyses elevated on the centrum; zygantral articular facets located in a common chamber rather than separate chambers; and single parazygantral foramina present lateral to the zygantral chamber, each foramen occurring in a small fossa.

*Etymology.*—The generic name refers to the Tuscahoma Formation.

*Tuscahomaophis leggetti*, new species

(Fig. 1–3)

*Diagnosis.*—Same as for the genus.

*Type specimens.*—Holotype: trunk vertebra, CM 47872 (Fig. 1), collected by K. C. Beard, A. R. Tabrum, G. R. Case, and J. J. Leggett. Paratypes: twelve trunk vertebrae—CM 47855 (one vertebra, Fig. 2); CM 47856 (six vertebrae); MSUVP 1334 (five vertebrae, Fig. 3), all collected at the same locality and horizon by the same collectors.

*Horizon.*—Latest Paleocene, Tuscahoma Formation.

*Type locality.*—CM loc. 517 (coordinates on file at CM), Lauderdale County, Mississippi.

*Etymology.*—The specific name is for J. J. Leggett, one of the collectors of the type material.

*Description.*—This description follows the order of views in Fig. 1–3. In posterior view, the holotype vertebra has the neural arch depressed with its lateral walls nearly vertical. The zygantral area is massive but structurally simple. There is a single, large zygantral chamber which houses the zygantral articular facets on

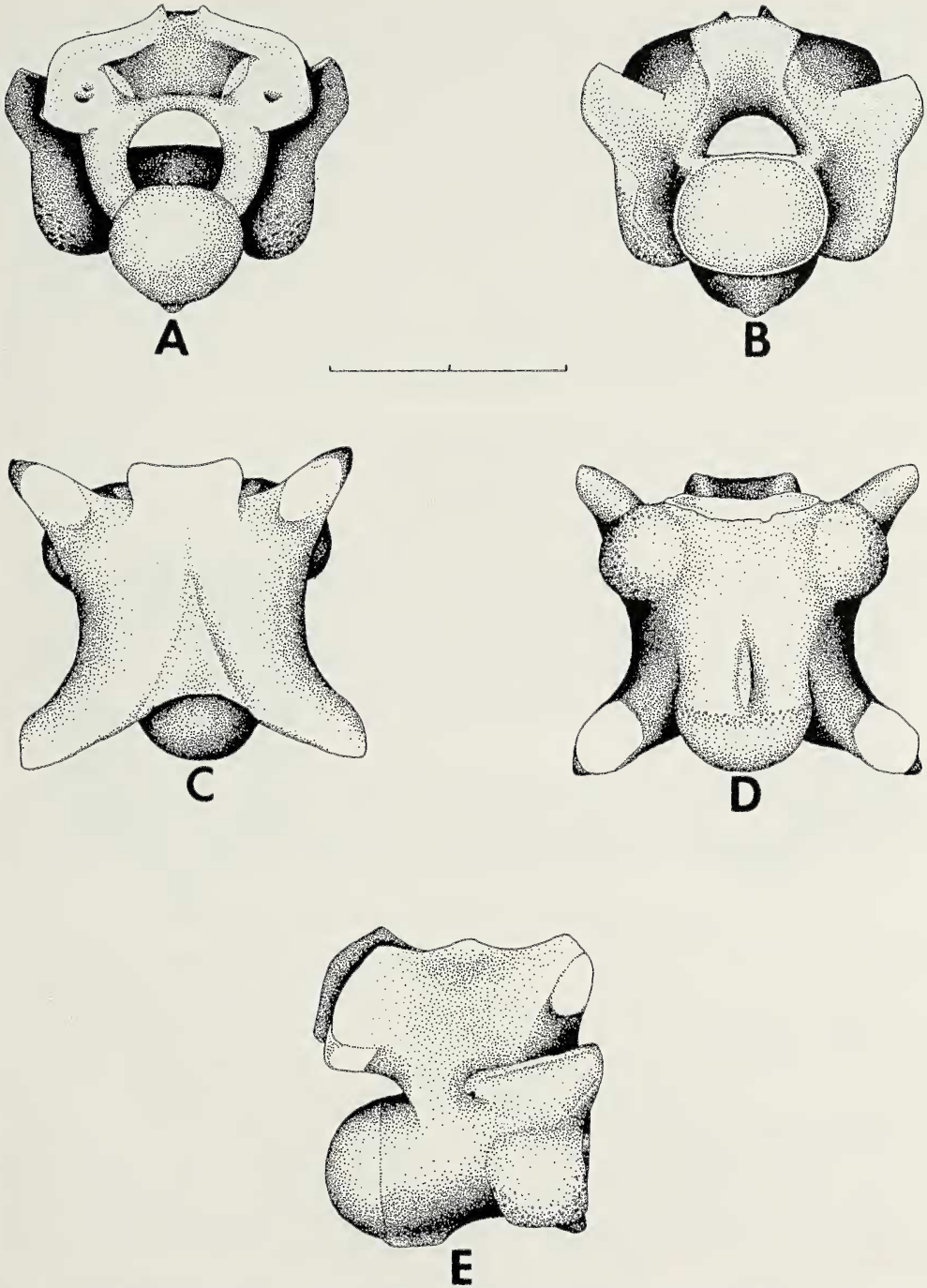
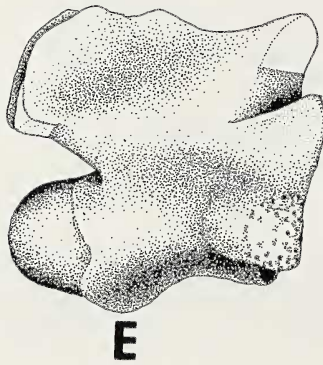
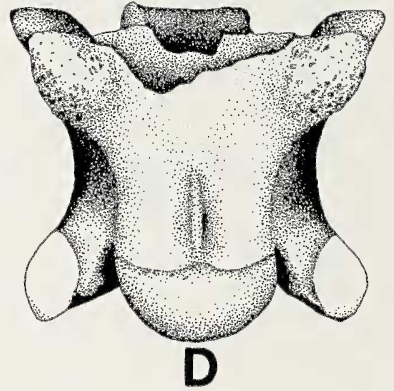
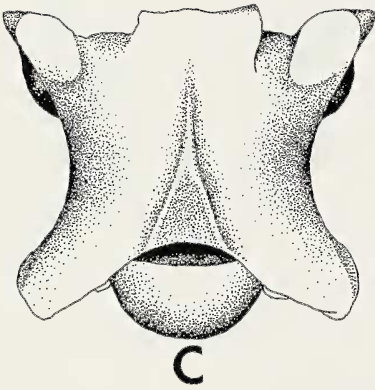
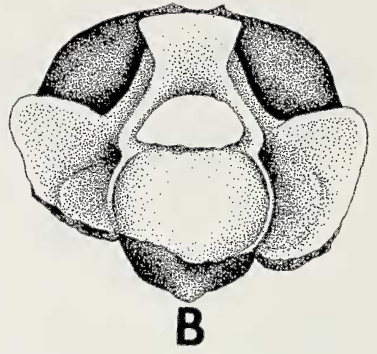
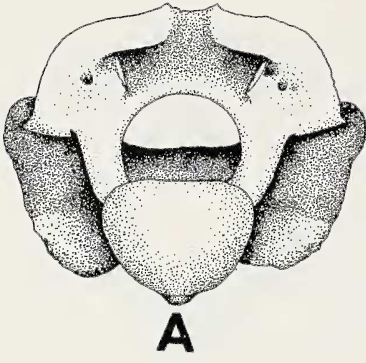


Fig. 1.—Holotype trunk vertebra of *Tuscahomaophis leggetti* nov. gen. et sp., CM 47872. A, posterior view; B, anterior view; C, dorsal view; D, ventral view; E, lateral view. The line equals 8 mm and applies to all views.



each side. Single parazygantral foramina lie in small fossae on either side of the zygantral chamber. The neural canal is round and is about two-thirds the size of the condyle. The condyle is rounded and very massive with its axis horizontal to the horizontal plane of the centrum. The paradiapophyses are massive and indistinctly divided. The hypapophysis is barely visible in this view.

In anterior view the zygosphene is massive. The neural canal is roughly triangular and is about two-thirds as large as the cotyle. Paracotylar foramina are present, the right is larger and more dorsally situated than the left. The cotyle is oval and wider than high. The prezygapophyses are tilted upward very sharply.

In dorsal view the vertebra is wider than long. There are no prezygapophyseal accessory processes. The faces on the prezygapophyseal articular facets are small and obliquely oriented. The zygosphene is distinctly set off from the neural arch and its anterior border is slightly concave. The neural spine is broken, but its remnants indicate that it was elongate and was wide posteriorly. Epizygapophyseal spines are absent.

In ventral view the paradiapophyses are massive, indistinctly divided, and in an elevated position on the centrum. The centrum is short, massive and its ventral surface is smooth except for the development of a small hypapophysis, which is thin and restricted to the posterior extent of the ventral centrum. The postzygapophyseal articular facets are ovaloid.

In lateral view the zygantral facets are ovaloid. The paradiapophyses are massive, indistinctly divided, and in an elevated position on the centrum. The prezygapophyseal buttresses have a sharp anterolateral border running from the anterodorsal border of the paradiapophyses to the anterolateral tip of the prezygapophyses and projecting beyond the prezygapophyseal facets. The small hypapophysis arises from the posterior one-half of the centrum. The condyle is massive.

There are few trenchant variations in the paratypes. Fig. 2 shows a paratype trunk vertebra of a snake that was smaller than that of the holotype. Fig. 3 shows a paratype trunk vertebra that is from a more anterior part of the vertebral column than that of the holotype; it has a somewhat more vaulted neural arch.

#### SYSTEMATIC RELATIONSHIPS AND PALEOECOLOGY

The classification used here follows Rage (1984) with the exception that the Madtsoiidae is considered a family rather than a subfamily.

In this system, snakes are divided into two suborders, Scelecoptidia and Alethinophidia. *Tuscahomaophis* trunk vertebrae represent the latter rather than the former in having a neural spine, a distinct hypapophysis, paracotylar foramina and a less depressed, much more complex vertebral structure.

*Tuscahomaophis* especially resembles some of the primitive alethinophidian families such as the Lapparentophiidae, Aniliidae, Xenopeltidae, Boidae, Madtsoiidae, Palaeophiidae, Acrochordidae, and Nigerophiidae in having a short, robust vertebral form, a massive zygosphene and zygantrum, a thick neural spine, a large cotyle and condyle, and in lacking prezygapophyseal accessory processes.

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Fig. 2.—Paratype trunk vertebra of *Tuscahomaophis leggetti* nov. gen. et sp., CM 47855, from a snake that was smaller than the holotype. A, posterior view; B, anterior view; C, dorsal view; D, ventral view; E, lateral view. The line equals 8 mm and applies to all views.

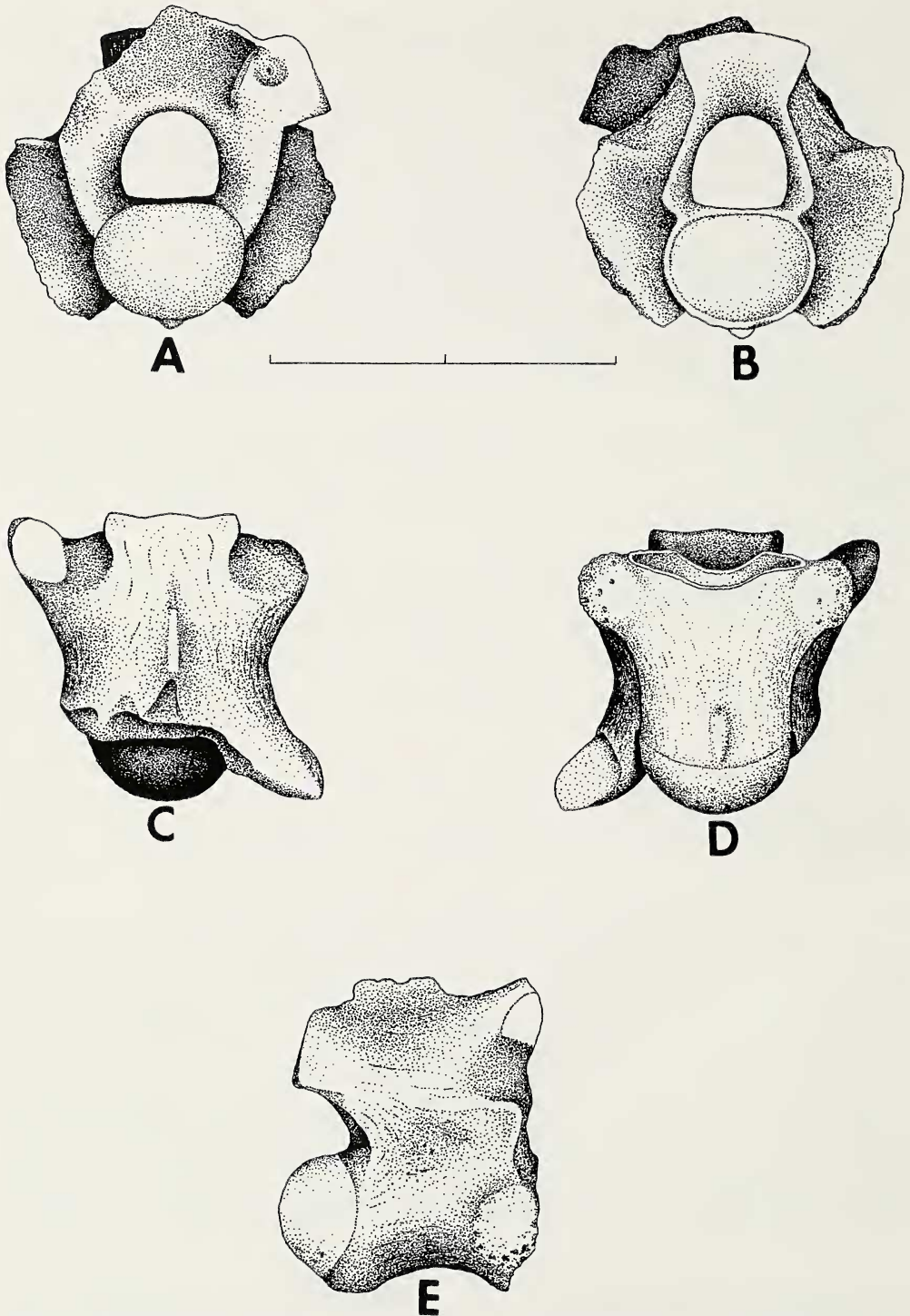


Fig. 3.—Paratype trunk vertebra of *Tusahomaophis leggetti* nov. gen. et sp., MSUVP 1334, from a more anterior part of the vertebral column than in the holotype. A, posterior view; B, anterior view; C, dorsal view; D, ventral view; E, lateral view. The line equals 8 mm and applies to all views.

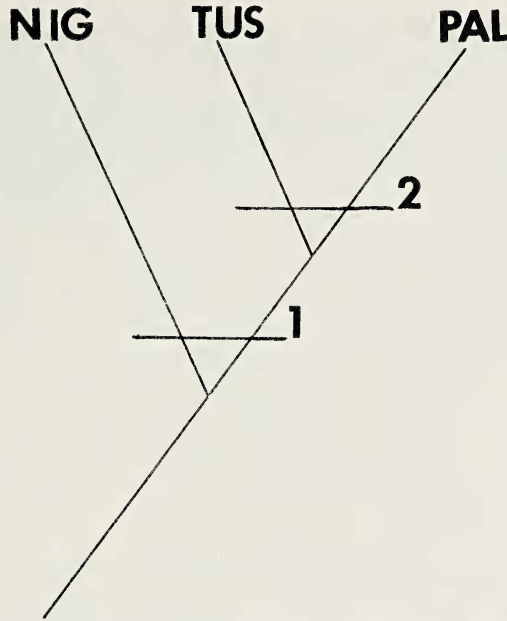


Fig. 4.—Hypothetical phylogenetic relationships of *Tuscahomaophis* (TUS) to Palaeophiidae (PAL) and Nigerophiidae (NIG). 1. Monophyly based on characters in paragraph 2 of diagnosis section. 2. Monophyly based on characters in paragraph 3 of diagnosis section. Characters are presumed to be synapomorphic although in some cases polarities are poorly known.

Among these primitive families, *Tuscahomaophis* most closely resembles the Palaeophiidae and, to a lesser extent, the Nigerophiidae (Fig. 4). It also shares a unique character with the Madtsoiidae (and one other undescribed genus), although a combination of other characters excludes it from any of these three families (see Diagnosis section).

*Tuscahomaophis* resembles the Palaeophiidae, especially the genus *Palaeophis*, in the following characters. It has a relatively smooth and unexcavated ventral centrum. Its condylar axis is horizontal or very slightly oblique to the horizontal plane of the centrum. It has a small, short hypapophysis that is confined to the posterior extent of the ventral centrum. The roof of the zygantrum is structurally simple. The neural arch is depressed, with its lateral walls mainly vertically oriented. The prezygapophyseal articular facets are small and oriented obliquely. The prezygapophyseal buttresses have a sharp anterolateral border running from the anterodorsal border of the paradiapophyses to the anterolateral tip of the prezygapophyses and projecting anterolaterally beyond the prezygapophyseal articular facets.

The other palaeophiid genus, *Pterosphenus* Lucas, has much enlarged, upswept pterapophyses; a strongly compressed vertebral form; and quite high neural spines, unlike the condition in *Palaeophis* and *Tuscahomaophis*.

*Tuscahomaophis* also shares some of the same characters with the Nigerophiidae that it does with the Palaeophiidae (see Diagnosis section), but it differs in having a shorter vertebral form, a relatively smooth ventral centrum, a much shorter hypapophysis and a depressed neural arch. An important character that *Tuscahomaophis* and the Nigerophiidae share is the lack of pterapophyses, which are a prominent feature of the Palaeophiidae.

*Tuscahomaophis* has one character that occurs only in the Madtsoiidae and

one other unnamed snake genus (Rage, 1984, and personal communication): the presence of a single foramen on either side of the zygantral chamber, with each foramen occurring in a small fossa. This character occurs in the madtsoiid genera *Gigantophis* Andrews, *Madtsoia* Simpson, *Alamitaophis* Albino, and *Patagoniophis* Albino. This character appears to be variable in the vertebral column in *Wonambi* Smith, a genus referred with doubt to the Madtsoiidae (Rage, 1984). It cannot be determined in the fragmentary trunk vertebra of *Rionegrophis* Albino, a genus that was considered a "probable" madtsoiid (Albino, 1986). The suite of presumably derived characters that *Tuscahomaophis* shares with the Palaeophiidae and Nigerophiidae and not with the Madtsoiidae, implies that the paracotylar foramina in small fossae were independently derived in *Tuscahomaophis*.

Considering the evidence, it seems reasonable to suggest that *Tuscahomaophis* is probably a sister group to the Palaeophiidae and that the Nigerophiidae is probably a sister group to both of the former taxa (Fig. 4). The relationships of *Tuscahomaophis* to the Madtsoiidae are doubtful. More osteological material, especially cranial elements, is necessary to establish the taxonomic relationships of *Tuscahomaophis* more firmly.

The presence of a large variety of fishes, including numerous species of selachians, at CM Locality 517 has led Case (1986) to suggest that the site likely represents an estuarine or riverine deposit. Three species of palaeophiid snakes (*Palaeophis casei*, *P. virginianus*, and *P. littoralis*) from CM 517 also are indicative of riverine or estuarine conditions (Holman et al., 1991). The morphological similarities between *Tuscahomaophis* and the Palaeophiidae (especially *Palaeophis*) implies that *Tuscahomaophis* was an aquatic snake that occupied similar habitats.

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